

STUDIES IN LIFE-HISTORIES OF AUSTRALIAN DIPTERA
BRACHYCERA.

PART I. STRATIOMYIIDAE.

No. 3. On the structure of the mouth-parts and pharynx of the larval
Metoponia rubiceps.

BY VERA IRWIN-SMITH, B.Sc., F.L.S., Linnean Macleay Fellow of the
Society in Zoology.

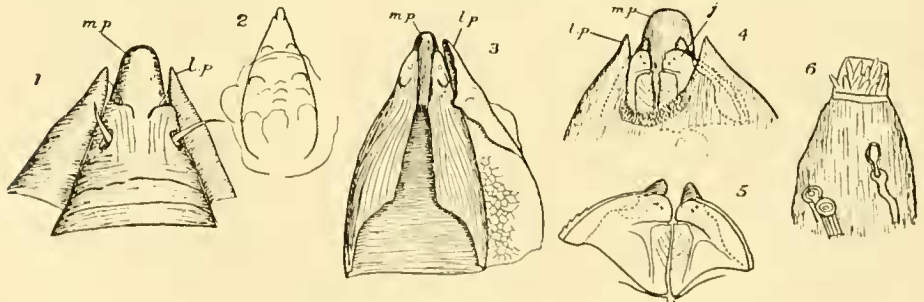
(Plate xxxiii., and twenty-six Text-figures.)

No satisfactory description exists of the mouth-parts of any larval *Stratiomyidae* other than a few aquatic species. Vancy (1902) and Jusbaschjanz (1910) have done some work on the genera *Stratiomyia* and *Odontomyia*; and Becker has taken the genus *Stratiomyia* as the type of the family *Stratiomyidae* in his general account of the mouth-parts of Dipterous larvae (1910). But many of the features present in this genus, such as the great development of tufts of hairs on the jaws, must be regarded as highly specialised adaptations to the aquatic mode of life, and a more typical form must be looked for in the soil-inhabiting species. Very few attempts have been made to study these in detail. Tragardh's description of *Pachygaster minutissima* (1914) contains a brief account of the head and mouth-parts, with several figures, which, unfortunately, are not very clear. He points out the difficulty of getting a good idea of these structures, and of their homology with those of other fly larvae. Indeed, most Dipterologists, from Brauer onwards, who have studied the larval forms, mention the great technical obstacles in the way of their elucidation. The parts are all very minute, and are composed of such dense chitin that the clearing, sectioning, or dissection of them seldom gives good results. The knowledge of the mouth-parts of the whole group of Diptera Brachycera is, for this reason, very meagre. Brauer, forty years ago, made an excellent comparative study (1883) of the material then at his disposal, and Becker has since contributed (1910) some additional information on the same subject, from the study of a few more representatives of the different groups. But he, too, draws attention to the paucity of the data on which to make generalisations and to interpret the nature of the separate mouth appendages. Therefore, until the larvae of all the families of Brachycera have been studied in greater numbers of species, and in greater detail, I do not think it possible to add anything of value in this connection; and, for this reason, I have not attempted, in the following description, to compare the various structures with those described in other Stratiomyid larvae, and in the larvae of any other of the Brachycera.

The *Stratiomyidae* belong to that group of fly larvae characterised by having parallel jaws, working upwards, or outwards, and downwards, as distinguished from those with opposing, horizontally moving mandibles. The adaptation accords with their method of obtaining nourishment by suction, instead of by biting and chewing; and the larval *Metoponia rubriceps*, which lives on the juices in the roots of grasses, shows this feature very well. A brief description of the mouth-parts is contained in the first paper of this series (Irwin-Smith, 1920). The present paper gives the results of more detailed morphological investigations.

Mouth-parts.

Bounding the upper side of the oral aperture is a smooth, cylindrical, peg-like process, the median process (*m.p.*). It is not movable, and is really the terminal apex of the shield-shaped sclerite which covers the greater part of the dorsal surface of the head (Text-fig. 2). At the base of the median process the lateral edges of the sclerite bend inward and downward into the interior of the head, forming a sort of internal skeleton, and enclosing a cavity which continues up into the median process (Text-fig. 3). The process appears to be a composite structure, formed by the fusion of a median and two side pieces. On the ventral side, where the fusion is incomplete, two longitudinal slit-like apertures communicate with the hollow interior of the process. Laterad of these are two downwardly directed knob-like projections. On the dorsal surface, the anterior extremity of each side piece is marked by a ridge, and immediately in front of this is inserted a fine hair (Text-fig. 1). A similar, but somewhat larger hair is situated further back, in a deep circular depression. The median process measures about 0.03 mm. across the tip, and 0.14 mm. from tip to base on ventral side. The whole sclerite, including the median process, and the internal ridges, is composed of very dense, dark brown chitin, and can be dis-



Text-figures 1-6.

1. Dorsal view of anterior end of head. (x 120).
2. External view of dorsal sclerite. (x 32).
3. Internal view of the same, with one lateral plate still attached. (x 66).
4. Ventral view of mouth parts. (x 120).
5. Mouth jaws. (x 166).
6. Portion of cuticular wall just below ventral processes showing glandular apertures (?). (x 320).

j, jaw; *l.p.*, lateral plate; *m.p.*, median process.

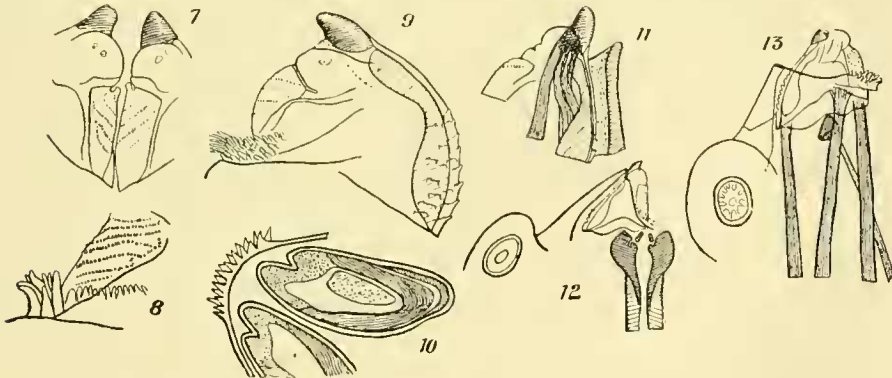
sected away from the remaining parts of the head in a single piece (Text-fig. 2). Posteriorly, it is connected up with the sides of the head by a stout, membranous cuticle, having an armour of hexagonal plates somewhat similar to those on the body (Text-fig. 3). Further up, it is firmly fused with the dense chitin which forms the lateral "bosses" and extends forward in the shape of two

sharply-pointed lateral plates (*l.p.*). These plates, although firmly united with the median process, in such a way as to allow of no separate movement, can be broken away from it fairly readily, when the parts are dissected out. From their hard, strong apices they extend downward in a deep curve, to unite in the ventral median line in a structure of much softer composition, which forms the ventral boundary of the oral aperture. Its edge is fringed with several rows of soft processes (Text-fig. 4).

Immediately below these processes, there is, in the cuticle, a group of what appear to be the openings of ducts. A pair of these is situated close to the centre line, with two more on each side a little further back (Text-fig. 6).

The lateral plates are hollowed out to form sheaths, or sockets, for the two movable mouth jaws (Text-figs. 5, 9). These jaws, although very minute, less than a tenth of a millimetre long, have a very complicated and interesting structure. In form they are somewhat conical, having a broad oval base (Text-fig. 10) and a pointed apex. The apex consists of a single, relatively large (0.026 mm. long) tooth of dense chitin, which rests on, and articulates with the chitinous internal framework which strengthens the back part of the jaw (Text-fig. 11). This framework serves, also, as the point of attachment for the muscles which move the tooth. With the exception of these chitin structures, and another chitin mass at the base, the entire jaw is composed of several distinctly marked off areas of clear, colourless composition.

Below the tooth is a soft, rounded, cushion-like swelling, having on its outer face two small, oval patches, which appear to be of the nature of sensory papillae. A deep groove separates this swelling from a plate which bears on



Text-figures 7-13.

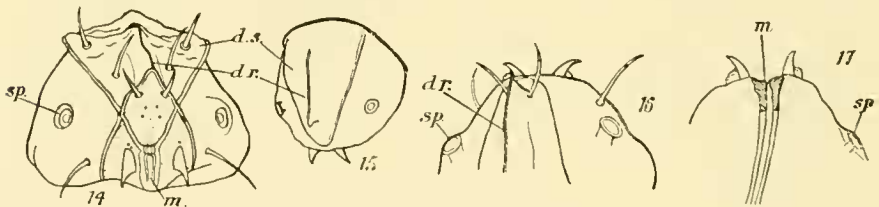
7. Inner edges of the two jaws. (x 280). 8. Denticles of jaw. (x 320). 9. Side view of entire jaw. (x 280). 10. Transverse section through lower part of jaws. (x 280). 11. Apical tooth of jaw, showing attachments of muscles which move it. (x 200). 12. Oral termination of pharynx, showing the pillars which support the jaws. (x 120). 13. Attachments of muscles which move the whole jaw. (x 120).

its outer face from five to seven transverse rows of minute denticles (Text-figs. 7, 8, 9). The denticle plate extends to that part of the jaw which is nearest to the opposite jaw, but does not continue round its inner face: so that the denticles of the two jaws are hardly opposable. On the back of the jaw, where it moves in the socket of the lateral plate, the cuticle is raised into a series of serrated ridges (Text-fig. 9).

The whole jaw is supported by its base on a central chitinous peg, which acts as a pivot on which the jaw can move with a rocking movement. The muscles which move it are shown in Text-fig. 13. They extend back through the head for some distance, to be inserted posteriorly in the head wall. Average measurements for the jaw are 0.088 mm. from apex to base, and 0.085 mm. in diameter from front to back.

The pivots on which the jaws work form part of the chitinous wall surrounding the anterior end of the pharynx. The oral aperture is situated just at the base of the median process, where the latter opens out into the internal cavity of the head (Plate xxxiii., fig. 1a) and here the strongly chitinised rim of the pharynx grows up on each side, in the form of a stout, curved, pointed pillar (Text-fig. 12) to support the jaw. Lying free between these, in the oral opening, are two very small blocks of chitin. The opening is quite concealed by the overlying jaws and processes, and is only revealed by careful dissection.

In his description of the mouth parts of Stratiomyid larvae which he had examined, Becker makes the statement that there is no median mouth opening, and that nourishment is taken in through the lateral slits in the walls



Text-figures 14-17.

Drawn from cast skins of first ecdysis.

14. Front view of head, showing terminal mouth, and jaws. (x 320). 15. General view of head, from antero-dorsal aspect. (x 190). 16. Anterior part of head, dorsal view. (x 320). 17. Internal view of same, showing pharynx. (x 320).

d.r., dorsal ridge; *d.s.*, dorsal sclerite; *m.*, mouth; *sp.*, spiracle.

of the median process which, he suggests, has been formed by the coalescence of upper and lower lips. That this is not the case with the larva of *Metoponia rubriceps* is very clearly shown by an examination of cast larval skins, found with the empty egg cases and newly hatched larvae. These skins have been described in the second paper of this series (Irwin-Smith, 1921). The cast of the head retains the original shape and position of all the parts, and is very interesting as showing an earlier stage of development than is seen in the hatched larva itself. In the cast skin the mouth opening is quite terminal in position, and is bounded only by the two stout jaws (Text-figs. 14-17). Of the lateral chitin plates, which afterwards ensheath them, there is here no trace. The dorsal sclerite is already well developed and clearly marked off by a thickened rim (*d.s.*). In the middle of the sclerite there is a longitudinal ridge (*d.r.*) which terminates towards the anterior end in a short, pointed outgrowth. This is evidently the rudiment of the median process. A careful examination of the position of the hairs surrounding it seems to show that the median process of the fully-developed larva is formed from it, by the overgrowth of this portion of the sclerite and a pushing forward of the process on to the part of the sclerite lying in front of it, and its fusion with the side walls. The skins being

very minute, the exact structure of the parts can only be made out with difficulty, under high magnifications; and for a full working out of the details of development, a complete series of the embryonic stages would be required. Unfortunately, I have been able to hatch out only one batch of eggs, and of these, have only the last stage, immediately before hatching, for examination. At hatching, the mouth parts of the larva differ very slightly from those of the older larvae. Some dozen or more skins were obtained, closely tangled up with the empty egg mass; and all show exactly the same stage of development.

In the casts, the terminal portion of the pharynx is already surrounded by a thickened outgrowth of chitin, but from this point the pharynx runs back through the head as a simple structure of uniform width (Text-fig. 17). None of the skins contain any trace of an internal chitinous skeleton, or indication of the presence of the masticatory apparatus, which is such a prominent and characteristic feature of the larva.

The Pharynx. (Plate xxxiii., figs. 1-5, and Text-figures 18-26.)

Vaney, Becker, and Jusbaschjanz have described this apparatus (called by them the "Schlundkopf") as it appears in the aquatic larvae which they examined; and Jusbaschjanz has studied it by means of transverse sections, and has given some figures of it. It is a highly complicated and beautifully adjusted piece of mechanism, and requires a good deal more study than has been given to it. The figures and descriptions already published are not very clear, but in *Metoponia rubriceps* the apparatus seems to differ somewhat, in form and structure, from those previously described. Satisfactory sections through this part of the larva are difficult to obtain. The chitin composing it is so dense and brittle as to defy all attempts to soften it sufficiently for the microtome, and the parts become shattered in the cutting. Dissections show the relationships of the various parts very well, but the study of transverse sections has necessitated much careful reconstruction, after detailed examination of long series of torn fragments.

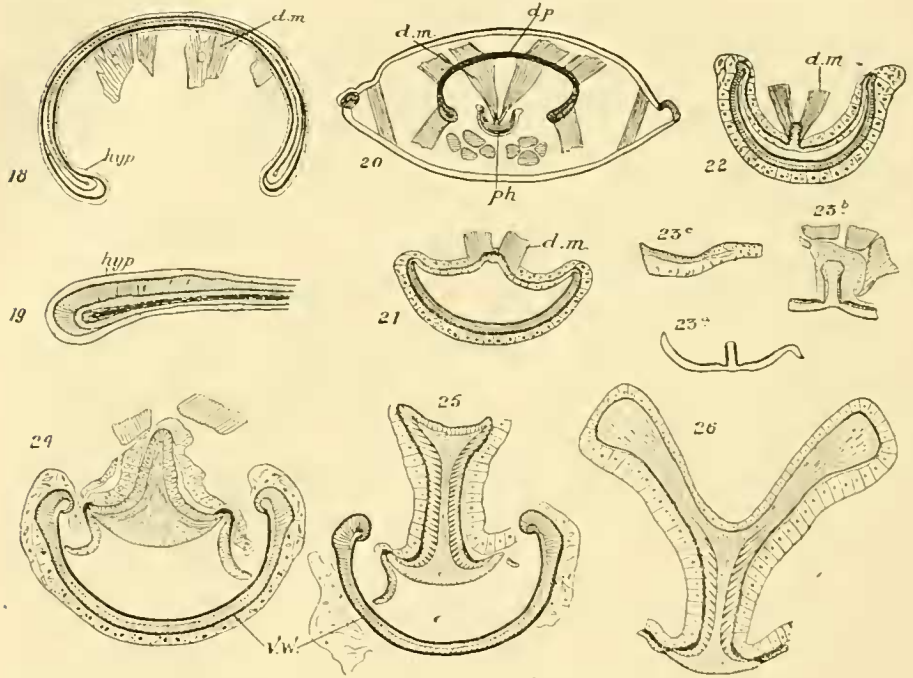
As in all Stratiomyid larvae, the dorsal sclerite of the head is continued back through the first thoracic segment as an internal skeleton in the form of a dorsally convex arch, the dorsal head plate (*d.p.*). It extends to the middle of the second segment, and is firmly held in position by means of powerful muscles attached to the body wall, which are shown in Text-fig. 20 and Plate xxxiii., fig. 1. Its ventral surface serves as the point of attachment for the dilator muscles of the pharynx (*d.m.*).

The pharynx (*ph.*) lies in the space between its lateral margins, and terminates posteriorly about the middle of the first segment, in the complicated masticatory apparatus already referred to. From this, the slender, thin-walled oesophagus passes straight back, below the dorsal plate, to open into the proventriculus at the level of the third thoracic segment (Plate xxxiii., fig. 5).

In transverse sections, stained with haematoxylin and eosin, the dorsal head plate is seen to consist of several layers of chitin (Text-fig. 18). In cutting, it frequently splits apart, along the middle line, into an upper and lower portion, of equal width, each part graduating from a pinkish colour on the inside to a dark yellowish brown on the outside; and in contact with the latter layer all round, dorsally and ventrally, is a layer of hypodermis. The lateral edges are rounded and thickened, with an additional layer of brown chitin along the upper surface (Text-fig. 19).

Anteriorly, the walls of the dorsal sclerite close in on the pharynx, but, so far as I can make out, there is no connection with it such as Jusbaschjanz

describes in the larvae of *Stratiomyia* and *Odontomyia*. The pharynx seems to lie free in the head cavity throughout its length. It is bow-shaped in transverse section, the string of the bow representing the dorsal wall (Text-fig. 21). Its ventral wall consists of a deeply arched piece of chitin, in two layers, the inner



Text-figures 18-26.

Transverse sections, showing the structure of dorsal head plate and pharynx.

18. Dorsal head plate. (x 66). 19. Lateral margin of head plate (x 160). 20. T.S. through 1st thoracic segment in region of spiracles. (x 32). 21. Pharynx, in region of head. (x 120). 22. Pharynx, further back. (x 120). 23a. Dorsal wall of pharynx. (x 130). 23b. Median ridge of same. (x 200). 23c. Portion of wall. (x 320). 24-26. Pharynx in region of "wing-bearer." (x 160).

d.m., dilator muscles of pharynx; *d.p.*, dorsal head plate; *hyp.*, hypodermis; *ph.*, pharynx; *v.w.*, ventral wall of pharynx.

pink, the outer yellowish-brown. Its lateral rims are strongly thickened and knob-like, and bounding it externally is a thick layer of hypodermis, consisting of a single row of cells.

The dorsal wall is of quite different composition, consisting of a substance which appears to be of a tough, elastic nature, and stains a deep blackish brown. It, also, is bounded externally by hypodermis. Along its median line are inserted the twelve or fourteen pairs of dilator muscles, which stretch between it and the dorsal wall (*d.m.*). By their contraction, these muscles evidently enlarge the cavity of the pharynx, and cause it to act as a powerful sucking apparatus.

The effect is augmented by the action of the peculiar mechanism at the posterior end of the pharynx. This is a greatly thickened chitin structure, wedge-shaped in ventral view, with broad base at the posterior end (Plate xxxiii., figs. 3, 4). It takes the place of the dorsal pharyngeal wall, and projects, by its downwardly curved under surface, into the space enclosed by the crescentic ventral pharyngeal wall. It is attached to the ventral wall on each side by a tough, dark-staining membrane, which appears to be similar in composition to the dorsal wall higher up. Dorsally it projects upwards and outwards in the form of two broad, stout, wing-like processes. Two powerful muscles, attached to each wing, extend backwards to be inserted in the posterior margin of the dorsal head plate (Plate xxxiii., figs. 1, 2). By the contraction of these muscles the upper part of the "wing-bearer" would be pulled outward and downward, while its base would work against the face of the ventral wall (Plate xxxiii., fig. 4). Apparently the reverse movement is effected by the elasticity of the ligaments connecting it with the pharynx anteriorly and laterally. I cannot detect the presence of antagonistic muscles, although such muscles are described by both Vaney and Jusbashjanz. But, as the "Schlundkopf," or masticatory apparatus, examined by them was globular in form, it will be seen that the details of its structure and relationships must necessarily be somewhat different. I have not been able to find anything to correspond with the lateral chitin plates which Jusbashjanz describes as projecting up from the basal plate of the wing-bearer, and connecting dorsally with the forked median plate which bears the wings. However, as I have experienced great difficulty in cutting this apparatus and have not been able to get a complete series of sections, I cannot speak with certainty of its structure throughout its entire length, or of the exact way in which it connects with the dorsal pharyngeal wall anteriorly. The figures of transverse sections given here represent careful reconstructions of those parts which I have been able to study in detail.

In the region of the pharynx immediately anterior to the "wing-bearer," the dorsal wall has the appearance shown in Text-figures 22, 23. There is here a short median process, to which the pairs of dilator muscles are attached, and which differs but little in composition from the rest of the dorsal wall.

Text-figures 24 to 26 represent transverse sections through different parts of the wing-bearer itself. The first tapers from the broad base to a point dorsally; the next shows a broadening and slight forking of the dorsal portion, the third the expansion into the two "wings." To the angles of the base are attached the ligaments which connect it with the ventral wall, here seen torn away from their connections in the sectioning. A broad layer of hypodermis covers the dorsal surface of the whole structure, and is continued along the connecting ligaments. The "wing-bearer" consists of an outer layer of chitin, staining dense brown, merging towards the interior into a clear pink, which encloses a central core of much lighter and apparently softer composition. It seems to be made up of a loose fibrous material, which is so transparent that, in surface view, the wing-bearer has the appearance of being hollowed out in the middle. But in transverse sections it is seen that this core broadens out into a base which is deeply convex.

In all the sections which I have examined, this base and the ventral plate present firm, smooth surfaces to each other, but in the posterior part of the apparatus there is a roughened appearance, suggesting denticles or other tooth-like structures, on a much denser foundation, which I did not succeed in sectioning.

The wing-bearer measures 0.33 mm. in length, with a breadth of 0.30 mm. to the tip of the wing.

References.

1910. BECKER, R.—Zur Kenntniss der Mundteile und des Kopfes der Dipteren Larven. *Zool. Jahrb. Anat.*, xxix., 281-314, Pl. 18, Figs. 19, 20.
1883. BRAUER, F.—Die Zweiflüger des Kaiserlichen Museums zu Wien. iii. Systematische Studien auf Grundlage der Dipterenlarven, nebst einer Zusammenstellung von Beispielen aus der Literatur über dieselben and Beschreibung neuer Formen. *Denkschr. k. akad. Wiss. Wien.*, xlvii., pp. 1-100, Pls. i-iv.
1920. IRWIN-SMITH, V.—Studies in life-histories of Australian Diptera Brachycera. Part 1. *Stratiomyidae*. No. 1. *Metoponia rubriceps* Maequart. *Proc. Linn. Soc. N.S.W.*, xlv., pp. 505-530, Pls. xvii-xviii., and 23 Text-figures.
1921. IRWIN-SMITH, V.—Ditto., No. 2. Further experiments in the rearing of *Metoponia rubriceps*. *Proc. Linn. Soc. N.S.W.*, xlvi., pp. 252-255, eight Text-figures.
1910. JUSBASCHJANZ, S.—Zur Kenntniss der Naehembryonalen Entwicklung der Stratiomyiden. *Jenaische Zeitsch.*, xlvi., pp. 681-736, 3 Taf.
1914. TRAGARDH, I.—Skogsentomologiska bidrag 1-5. *Entom. Tidskrift, Uppsala*, xxxv., pp. 188-209. (*Pachygaster minutissima* Zett., an under bark levende stratiomyid, pp. 192-196, Figs. 3-5).
1902. VANEY, C.—Contributions à l'étude des larves et des métamorphoses des Diptères. *Ann. Univ. Lyon.*, N.S., I., Fase. 9, 178 pp., 4 Plates.

EXPLANATION OF PLATE XXXIII.

Sucking apparatus of larva of *Metoponia rubriceps*.

- Fig. 1. Dorsal view of head and 1st thoracic segment, showing systems of muscles controlling dorsal head plate and pharynx. (x 48).
- Fig. 1a. Oral termination of pharynx. (x 190).
- Fig. 2. Lateral view of dorsal head plate and muscles of pharynx. (x 48).
- Fig. 3. Ventral view of posterior end of pharynx, showing wing-bearer. (x 100).
- Fig. 4. Lateral view of same. (x 100).
- Fig. 5. Anterior half of larva, giving a general view of the anterior portion of the alimentary system. (x 15).

c., chitin support for jaw; *d.*, dorsal muscles of head plate; *d.m.*, dilator muscles of pharynx; *d.p.*, dorsal head plate, *e.*, edge of interual skeleton of dorsal sclerite; *oc.*, oesophagus; *pv.*, proventriculus; *v.*, ventral muscles of head plate; *w.*, muscles of wing-bearer; *w.b.*, wing-bearer; *v.w.*, ventral wall of pharynx.